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Wolves facilitate the recovery of browse-sensitive understory herbs in Wisconsin forests

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We asked whether wolf re-colonization would facilitate increased growth and reproduction of three browse-sensitive plant species. We hypothesized plant size and the proportion of reproductive individuals would be lowest in areas with no wolves, intermediate where wolves had been present for 4–6 years, and highest where wolves had been present for 12–13 years. Two plant species exhibited significantly greater reproduction where wolves were present for 12–13 years. Mean leaf size of indicator plants was significantly greater in areas where wolves were present for 12–13 years, as compared with that in areas where wolves were not present or were present for 4–6 years, but the effect size appears small. While the return of wolves to this region is likely to benefit browse-sensitive plant species, our findings suggest that wolf recovery will not generate a trophic cascade of sufficient magnitude to halt or reverse the loss of plant diversity in the Great Lakes region in the near term.

Introduction

Following the extermination of predators and the enactment of restrictive game laws, white-tailed deer (*Odocoileus virginianus*) populations grew and their browsing resulted in major changes in forest community composition and structure throughout eastern North America (Côté *et al.* 2004). Deer browsing have been implicated in shifting community compositions reducing the abundance of palatable and non-resistant species to less palatable and resistant species (Gill 1992, Husheer *et al.* 2003, Rooney 2009). Repeated browsing of palatable and non-resistant herbaceous species can result in shorter stature, reduced growth and reproduction, truncated size structures, and population declines (Anderson 1994, Rooney and Gross 2003, Balgooyen and Waller 1995). Changes in plant community structure and composition following deer browsing can indirectly alter composition of animal assemblages, as is seen in birds (Allombert *et al.* 2005, Martin *et al.* 2011).

Wydeven *et al.* (2009) provide a brief history of gray wolves (*Canis lupus*) in Wisconsin. Prior to European settlement, there was sufficient prey to support 3000–5000 wolves in the state. Wolves were extirpated by 1960, and began recolonizing from Minnesota in the mid-1970s. Between 1980 and 2007, the wolf popu-

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lation grew from 25–28 individuals to 540–577 individuals (35.5 wolves per 1000 km^2). Wolves are now widely distributed across the northern third of the state. Pack locations and sizes have been mapped and monitored using radio-collars and winter track surveys since 1979 (Wydeven *et al*. 2009). The combination of extensive data and monitoring of a recovering wolf population, regionally-high deer densities, and impacted plant populations (Rooney *et al*. 2004) makes Wisconsin an ideal natural experiment for investigating trophic cascades.

Studies from western North America have demonstrated the effects recovering wolf populations can have on tree recruitment dynamics (Beschta and Ripple 2009). The reintroduction of wolves to Yellowstone National Park, for example, appears to have released aspen (*Populus tremuloides*) and willow (*Salix* spp.) from elk (*Cervus elaphus*) herbivory. The question of whether wolves generate trophic cascades in midwestern forests is largely unexamined. In years with high snowfall, wolves have influenced the growth rate of balsam fir (*Abies balsamea*) on Isle Royale by depressing moose abundance on the island (McLaren and Peterson, 1994, Post *et al*. 1999). However, it is unclear whether this trophic cascade is the exception or the rule in mainland Wisconsin forests.

In this study, we determined whether the recolonization of wolves could facilitate increased growth and reproduction of browse-sensitive plant species. To do this, we compared vegetation in areas that had wolves for three different periods of time. We compared areas without wolves with areas that established wolf packs for 4–6 years and for 12–13 years. We measured individual plant size, population size-structure, and the proportion of reproductive individuals of three herbaceous deer browse indicator species: *Polygonatum pubescens*, *Clintonia borealis*, and *Trillium grandiflorum* (Anderson 1994, Balgooyen and Waller 1995, Augustine and Frelich 1998, Kirschbaum and Anacker 2005, Rooney and Anderson 2009). We hypothesized plant size, size structure variation, and the proportion of reproductive individuals would be lowest in areas with no wolves and highest where wolves had been present for 12–13 years.

Material and methods

Site selection

Wolf pack locations have been mapped annually by the Wisconsin Department of Natural Resources (WIDNR) since 1979, and are maintained in a geographic information system. Annual shapefiles were overlayed in ArcGIS in order to determine how long an area was occupied by a wolf pack. Individual packs were selected for study based on a time criteria (either wolves continuously occupied the area for 4–6 years or 12–13 years). This created three treatments: no wolf impact, low wolf impact, and high wolf impact. Once a pack was selected, random points within its boundaries were chosen using ArcGIS and the coordinates recorded.

Each potential site was visited and cruised to determine that forest types were similar in age and composition, and contained populations of *P. pubescens*. *Polygonatum pubescens* is common throughout northern Wisconsin and was initially used as a focal species. Where they co-occurred, we collected data from *Clintonia borealis* and *Trillium grandiflorum* populations (measurement details are provided below). However, the absence of one or both of these species did not constrain our site selection procedure. Once the sites were deemed suitable, we randomly selected two packs from our list of wolf occupancy for 4–6 years, and two packs from our list of wolf occupancy 12–13 years. We established two sites within the territorial boundary of each pack.

Wolf-free sites were selected in a manner similar to sites with wolves. We used an ArcGIS map overlay to identify and select potential non-wolf sites. Potential non-wolf sites were selected in areas where the closest wolf pack boundary was located at least 5 km away. Forest types were similar in age and composition, and contained populations of *P. pubescens*. Four non-wolf sites were chosen for inclusion in the experiment.

Field methods

Surveys were conducted in June 2008 and 2009. A transect consisting of five 10 × 10 m plots

each separated by 20 m. Each transect was located at least 30 m from the nearest road or ATV trail road, with most transects established parallel to a road or trail. Plots were systematically sampled for *P. pubescens* until either all *P. pubescens* plants were measured (*see* details below), or alternatively, when 200 plants were measured. We required a minimum of 50 individuals per site for analysis. Consequently, not all sites were used in each analysis. A total of 1268 *P. pubescens* were surveyed at eight sites (three no-wolf, two 4–6 year wolf, and three 12–13 year wolf sites). We used the same procedure when sampling *T. grandiflorum* and *C. borealis*. In total, we measured 476 *T. grandiflorum* total at three sites (1 per wolf occupancy treatment) and 558 *C. borealis* at 4 sites (two no-wolf, one 4–6 year, and one 12–13 year).

Within each plot, we counted the number of leaves for each *P. pubescens* and recorded if the plant was reproductive. The number of leaves per plant (x) is directly related to total leaf area, y ($y = 1.50x$, $r^2 = 0.70$, $n = 49$; Bouchard 2009), so we used leaf count as a proxy for leaf area and hence plant size. We collected more detailed measurements to estimate leaf area of *T. grandiflorum* and *C. borealis*. For both species, the length and width of each leaf (in mm), which were converted into total leaf area using regression analysis ($y = e^{1.00\ln(\text{length} \times \text{width}) - 0.58}$, $r^2 = 0.99$, $n = 29$ for *T. grandiflorum*; $y = e^{1.06\ln(\text{length} \times \text{width}) - 0.91}$, $r^2 = 0.96$, $n = 57$ for *C. borealis*). The number of reproductive plants was also tallied for *T. grandiflorum* and *C. borealis*.

Data analysis

To determine the top-down influence of wolves on plant reproduction, we pooled flowering data across all sites within each wolf treatment. We assessed differences among treatments were analyzed using Yates' χ^2 goodness of fit tests.

To determine the effects of wolf occupancy duration on average leaf area of each species, we computed mean leaf area (A) in each wolf treatment. Measurements for each plant species were pooled for each wolf treatment. We performed analyses for three pairwise comparisons: "no wolves" and "wolves present 4–6 years," "no wolves" and "wolves present 12–13 years," or "wolves present 4–6 years," and "wolves present 12–13 years." In each case, we assume that areas with wolves for a longer period of time reflect a greater wolf impact, and areas without wolves or with wolves for a shorter period of time reflect a lower wolf impact. We then computed the log response ratio L for the leaf area of each species where $L = \ln(A_{\text{more wolf impact}}/A_{\text{less wolf impact}})$. When $A_{\text{more wolf impact}} = A_{\text{less wolf impact}}$, $L = 0$. Negative values of L indicate smaller plants in areas with less wolf impact, while positive values indicate larger plants in areas where wolves have been present for a longer period of time. A 95% confidence interval (CI) was calculated for each species L to determine if it differed from zero.

We combined results from all plant species to examine the used techniques developed for meta-analysis. Data from each species were combined to create a mean effect size, following the procedures outlined in Hedges *et al*. (1999). To account for among-species variation in effect sizes, we combined effect sizes from each plant species to calculate the mean effect size, or overall effect. The effect size of each plant species was first weighted by their inverse sampling variance plus a constant, q. The computation of q is derived from homogeneity analysis and represents variability across population effects (Hedges *et al*. 1999). To determine if the mean effect size differed from zero, we constructed 95% CIs. We considered top-down effects from wolves statistically significant if 95% CIs did not include zero.

Results

As compared with areas without wolves, plants growing in areas with wolves for a period of 4–6 years generally did not show any directional trends. The mean size of *P. pubsecens* plants was 36% greater in the 4–6 year wolf treatments than the non-wolf treatment. This difference was significant ($p < 0.05$; Fig. 1). However, the proportion of reproductive *P. pubescens* plants (27 of 327, or 8.3%) in the 4–6 year wolf treatments was not significantly different than the propor-

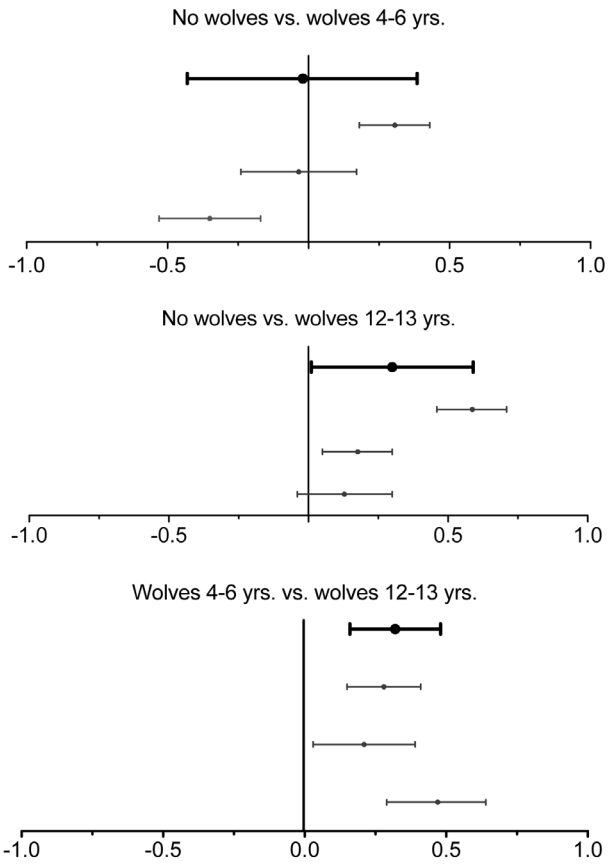

Fig. 1. Log response ratio (ratios of leaf area at sites with wolves for a longer time period relative to a shorter time period or wolf absence) and 95% confidence intervals for all species combined (thick line), *Polygonatum pubescens* (top thin line), *Clintonia borealis* (middle thin line), and *Trillium grandiflorum* (bottom thin line). Positive values indicate larger plants where wolves have been present for a longer period of time. Confidence intervals that intercept zero indicate no significant difference ($p > 0.05$).

tion (37 of 479, or 7.2%) in the no-wolf areas ($\chi^2 = 0.1$, df = 1, $p = 0.78$). The mean leaf area of *C. borealis* plants was 3% smaller in the 4–6 year wolf treatments than the non-wolf treatment, but this difference was not statistically significant (Fig. 1). None of the 94 plants were reproductive in the 4–6 year wolf treatments, compared to zero of 301 in the non-wolf treatment. The mean leaf area of *T. grandiflorum* plants was 30% smaller in the 4–6 year wolf treatments than the non-wolf treatment, and this difference was statistically significant ($p < 0.05$; Fig. 1). There were no reproductive *T. grandiflorum* plants in the 4–6 year wolf treatment, but 7.8% of the 191 plants were reproductive in no-wolf areas ($\chi^2 = 12.7$, df = 1, $p < 0.001$).

As compared with areas without wolves, plants growing in areas with wolves for a period of 12–13 years showed some signs of recovery. Mean size of *P. pubsecens* plants was 80% greater in the 12–13 year wolf treatments than the non-wolf treatment (Fig. 1). This result was statistically significant. Additionally, the proportion of reproductive *P. pubescens* plants (79 of 433, or 18.2%) in the 12–13 year wolf treatments was more than twice the proportion (37 of 479, or 7.2%) in the no-wolf areas ($\chi^2 = 21.7$, df = 1, $p < 0.001$). Mean size of *C. borealis* plants was 13% greater in the 12–13 year wolf treatments than the non-wolf treatment (Fig. 1). This result was statistically-significant. However, only 1 plant of 200 was reproductive in the 12–13 year wolf treatment. Zero of 338 plants was reproductive in the no wolf treatment. Mean leaf area of *T. grandiflorum* plants in the 12–13 year wolf treatments was also 13% greater in than the non-wolf treatment, but this was not significantly different (Fig. 1). Of 191 *T. grandiflorum* plants in the 12–13 year wolf treatment, 7.3% (14 of 191) were reproductive. This did not significantly differ from the 7.8% reproductive (15 of 191) in no-wolf areas ($\chi^2 = 0.0$, df = 1, $p = 1.0$).

As compared with areas with wolves for 4–6 years, plants growing in areas with wolves for a period of 12–13 years were generally larger and more likely to flower. Mean size of *P. pubsecens* plants was 30% greater in the 12–13 year wolf treatments than the 4–6 year wolf treatment (Fig. 1) and were 2.2 times more likely to flower ($\chi^2 = 14.66$, df = 1, $p < 0.001$). Mean size of *C. borealis* plants was 24% greater in the 12–13 year wolf treatments than the 4–6 year wolf treatment ($p < 0.05$; Fig. 1). Because only a single plant was in flower, the influence of wolves on reproduction could not be assessed. Mean size of *T. grandiflorum* plants was 61% greater in the 12–13 year wolf treatments than the 4–6 year wolf treatment (Fig. 1), and plants were more likely to flower ($\chi^2 = 5.8$, df = 1, $p = 0.02$). No *T. grandiflorum* plants flowered in the 4–6 year wolf treatment.

Meta-analysis allowed us to combine the data across species and examine the net effect. When the mean leaf sizes of plants were combined into a single effect size, there was no significant effect of the 4–6 year wolf treatment on plant size relative to areas without wolves ($p > 0.05$; Fig 1). The combined effect size of all three indicated a significantly larger leaf size when wolves were present for 12–13 years relative to no wolves, as the lower bound of 95%CI was greater than zero (Fig. 1). The largest differences in mean leaf size were found between the 4–6 year wolf treatment and the 12–13 year wolf treatment. The mean leaf size was significantly greater in the 12–13 year wolf treatment for all three species, and the combined effect size was significant (Fig. 1).

Discussion

The re-colonization of the Great Lakes region by wolves can be represented as a type of chronosequence (Rooney and Anderson 2009). Packs became established in some areas 15 years ago, while other areas have been colonized in the past few years. Time since re-colonization by wolves was associated with a modest increase in growth and reproduction of browse-sensitive indicator plant species. Mean leaf size of indicator plants was significantly greater in areas where wolves were present for 12–13 years, as compared with that in areas where wolves were not present. The magnitude of the effect appears small.

Reproduction of browse-sensitive species usually declines in response to herbivory (Côté *et al*. 2004, Kirschbaum and Anacker 2005), but reproduction was a poor indicator of a response in this study. While over 1000 plants were sampled across the three species, we were unable to draw statistically-reliable conclusions about reproduction of *C. borealis*. Our other species were most likely to flower in areas with wolves for 12–13 years.

Meta-analysis of plant sizes indicated that plants growing in the 12–13 year wolf treatment were significantly larger than plants growing in the no-wolf treatment, but there was significant heterogeneity among species. There was an even greater difference between growing the 12–13 year wolf treatment relative to plants growing in the 4–6 year wolf treatment. Browse-sensitive plant species performed most poorly at sites with wolves present for 4–6 years. Indeed, it appears that plants growth and reproduction is higher with no wolves at all, relative to wolves present for 4–6 years. Initially, this result puzzled us. In retrospect, however, we realized that our initial hypothesis was faulty. When colonizing a new area, wolves select areas with high deer densities (Fuller 1989, Potvin *et al*. 2005). Our "no wolves" sites were probably located areas with fewer deer than elsewhere in the landscape. We would have been wiser to sample vegetation in areas that had wolves for a brief period of time, such as 1–2 years, instead of areas with no wolves. Such areas may have served more effectively as "high deer impact" sites within the wolf re-colonization chronosequence we wished to explore.

The magnitude of plant recovery from deer browsing is much less than that found in the aspen and cottonwood of Yellowstone after wolves were re-introduced (Ripple *et al*. 2001, Ripple and Beschta 2003, Beschta and Ripple 2009). The differences in the magnitudes of vegetation response between our study and those from Yellowstone could simply be the result of a few factors. Herbaceous plants growing in a shaded forest understory do not show the same growth rate as woody species growing in sunny riparian areas when released from herbivory. Elk

concentrate their foraging in discrete areas of the landscape with high quality forage. White-tailed deer have high quality food distributed more evenly across the landscape, which could make their daily movements more unpredictable to predators (Rooney and Anderson 2009). It is quite possible that trophic cascades are not biologically important in the Great Lakes. Alternatively, 12–13 years is an insufficient amount of time for trophic cascades to become apparent.

There were two key limitations of our study design that could have affected our results. First, we did not statistically control for differences in wolf pack sizes in our study areas. Wolf pack sizes are estimated every year, but pack sizes change seasonally and from year to year. Between 1995–2007, mean pack size was 3.1 ± 0.3 wolves (Bouchard 2009). Second, we did not have good deer population density estimates from our study areas. Wisconsin estimates deer densities for a deer management unit, and these units are ~1000 km^2. Between 1995–2007, overwintering densities averaged 11.2 ± 1.3 deer km^{-2} in the study area (Bouchard 2009). We have no information about deer density at the spatial scale of study plots. Both limit the strength of inferences we can draw.

High deer densities throughout much of the upper Great Lakes region continue pose a challenge to conservation efforts. Deer browsing contributes to the erosion of plant diversity (Rooney *et al*. 2004). This in turn could lead to additional indirect effects on insects, birds, and other species (Rooney and Waller 2003). While the return of wolves to this region is likely to have modest benefits that accrue to plants (Callan *et al*. 2013), our findings do not suggest that the current wolf population is sufficient to halt or reverse the loss of plant diversity in the Great Lakes region in the near term. The recovery of browse-sensitive understory herbs in Wisconsin forests is dependent on the severity of previous browsing and the degree to which browsing is reduced (Kirschbaum and Anacker 2005, Rooney *et al*. 2004).

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